

New Specimens of the Oldest Fossil Platyrrhine, *Branisella boliviana*, From Salla, Bolivia

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ABSTRACT During the 1992 and 1993 field seasons, several new specimens of *Branisella boliviana*, the oldest fossil platyrrhine, were discovered in the late Oligocene deposits at Salla, northwestern Bolivia. The new materials are two maxillary fragments and seven mandibular fragments, including P³ and P₂, neither of which have previously been recovered. All new and previously reported materials, including the holotype and referred specimens, were apparently recovered from the same horizon, called the *Branisella* zone (MacFadden et al. [1985] J. Geol. 93:223–250; MacFadden [1990] J. Hum. Evol. 19:7–21.

The crown morphology of the newly discovered upper and lower premolars suggests that *Branisella* has a close affinity with callitrichines. A detailed examination of all molar specimens suggests that “*Szalatavus attricuspis*,” which was recovered at Salla in 1981 and described as a new genus by Rosenberger et al. (1991), is a junior synonym of *Branisella*. The *Branisella*-like upper molar, in which a small hypocone is preserved on the poorly developed distolingual cingulum, is a shared-derived character with callitrichines and does not correspond to the primitive state for platyrrhine phylogeny. The ancestral upper molar morphotype for platyrrhines should have a moderate to large hypocone and a well developed talon area. © 1996 Wiley-Liss, Inc.

The oldest known fossil platyrrhine, *Branisella boliviana*, is known from the late Oligocene–early Miocene deposits of the Salla-Luribay basin, northwestern Bolivia (Figs. 1,2). The first specimen, a fragmentary maxilla, was described in the 1960s (Hoffstetter, 1969), only four additional referred specimens (one maxillary and three mandibular fragments) have been reported (Rosenberger, 1981; Wolff, 1984; Rosenberger et al., 1991b). All these specimens are fragmentary jaws, mostly with well worn teeth, so the morphological characteristics of this species have not yet been established. Some workers have emphasized its morphological resemblance to living squirrel monkeys, *Saimiri* (Hoffstetter, 1969, 1974; Szalay and Delson, 1979; Gingerich, 1980; Wolff, 1984; Conroy, 1990), and others to omomyids or callitrich-

ines (Gingerich, 1980; Rosenberger et al., 1991b). The shortage of materials has led to controversy about the phyletic position of *Branisella*. Recently some workers classified Salla specimens into two taxa, *Branisella boliviana* and “*Szalatavus attricuspis*” (Rosenberger et al., 1990, 1991b), but the validity of the latter taxon is far from confirmed.

During the 1992 and 1993 field seasons, several new primate fossils were recovered at Salla. All of them were collected from almost the same horizon, known as the *Branisella* zone (MacFadden et al., 1985; MacFad-

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Fig. 1. Map of Bolivia showing location of Salla.

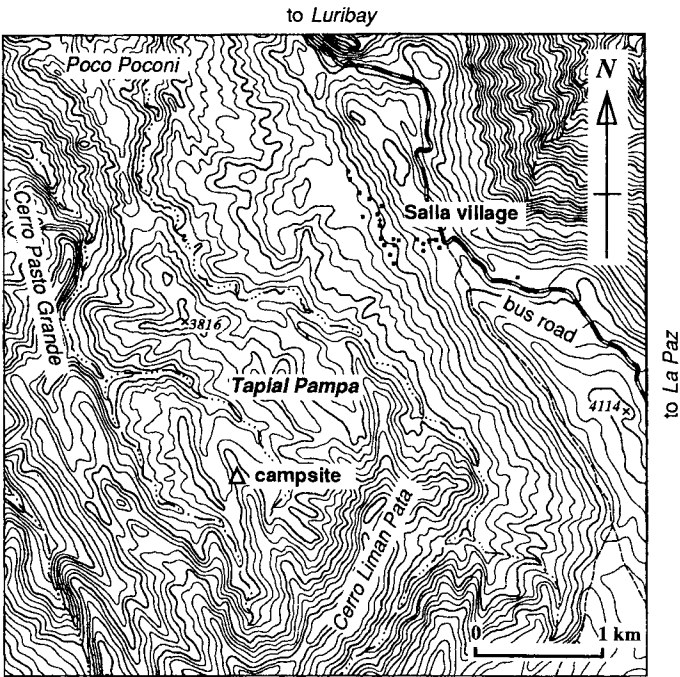


Fig. 2. Detailed map of Salla. Δ, campsite.

den, 1990). New materials described in this report include callitrichine-like upper and lower premolars (P^3 and P_2) and suggest an interesting phyletic position for *Branisella* during the early evolution of primitive platyrrhines.

In this paper, "callitrichines" include *Cebuella*, *Callithrix*, *Saguinus*, *Leontopithecus*, and *Callimico*; "pitheciines" include *Pithecia*, *Chiropotes*, and *Cacajao*; and "atelines" include *Alouatta*, *Ateles*, *Brachyteles*, and *Lagothrix*. No other higher taxa are discussed.

LOCALITY AND HORIZON

The new materials were recovered from the same area, Tapial Pampa of the Salla-Luribay basin, about 90 km southeast of La Paz, Bolivia (Figs. 1,2). During the 1992 field season, four specimens (MNHN-Bol-V 3460, 3463, 3464, and 3465) were collected from a site called Los Cactus (which is a small basin of about 10×10 m located some 300 m from the campsite), and two maxillary fragments (MNHN-Bol-V 3466 and 3467), attributed to the same individual, were collected midway between the campsite and Los Cactus. During the next field season, 1993, two mandibular fragments (MNHN-Bol-V 3471 and 3473) were collected from the opposite side of the ravine of Los Cactus, and two specimens (MNHN-Bol-V 3468 and 3469) were recovered just beside the campsite. All of these sampling points are designated as being at the same level, in the *Branisella* zone (MacFadden et al., 1985; MacFadden, 1990). Apart from the type specimen, other referred specimens (UF27887, 27888, and 91399) were also collected from almost the same horizon (Wolff, 1984; MacFadden et al., 1985; Rosenberger et al., 1991b).

The Salla beds consist of fluvatile reddish clays and silts, and contain a fauna assigned to the Deseadan Land Mammal Age (McKenna, 1980; MacFadden et al., 1985; MacFadden, 1990). Several workers have calculated radioisotopic ages from these deposits: 26.4 ± 1.0 Ma by the K-Ar method, and 22.0 ± 2.0 and 22.2 ± 1.9 Ma by the fission-track method (MacFadden et al., 1985); 25.1 ± 0.7 , 27.9 ± 0.9 , 27.2 ± 0.9 , and 28.0 ± 0.9 Ma by the K-Ar method, and 24.2

± 3.6 , 23.5 ± 2.2 , and 34.5 ± 4.0 Ma by the zircon fission-track method (Naeser et al., 1987); and 27.6 ± 1.6 and 25.0 ± 1.5 Ma, and 26.1 ± 1.9 , as well as 24.0 ± 1.5 Ma by the zircon fission-track method (Hayashida and Danhara, 1985). Among these absolute ages, it is very significant that there is concordance between two K-Ar dates (26.4 ± 1.0 and 25.1 ± 0.7 Ma), which were acquired independently from the same level just below the *Branisella* zone (MacFadden et al., 1985; Naeser et al., 1987; see also McRae, 1990). The results of these studies suggest a late Oligocene to early Miocene date for the Salla deposits, and an age of about 25–26 Ma for the *Branisella* zone. On the basis of the paleomagnetic study, MacFadden et al. (1985) suggest a late Oligocene date and McRae (1990) advocates an earliest Miocene date for the Salla beds, but the absolute age for the *Branisella* zone will not be changed.

SYSTEMATIC PALEONTOLOGY

Specimens are of the order Primates, suborder Anthropeidea, infraorder Platyrrhini, family incertae sedis: *Branisella boliviana* Hoffstetter, 1969 (including "*Szalatavus atricus* Rosenberger et al., 1991b").

Holotype

This is a left maxillary fragment with P^4 – M^2 and roots of $P^{2,3}$, housed in the Muséum National d'Histoire Naturelle (there is no specimen number described; Fig. 3d). For referred specimens and new materials, see Table 1.

Locality and horizon

All new and referred specimens but one were recovered from the *Branisella* zone of MacFadden (1990), in Tapial Pampa of the Salla-Luribay basin, about 90 km southeast of La Paz, Bolivia. Only one specimen (MNHN-Bol-V 3471) was collected approximately 6 m below the *Branisella* zone, although, as judged from its location, it may have fallen down from the higher level.

Distribution

Specimens are from the late Oligocene (to early Miocene?), Deseadan Land Mammal Age, about 26.4 ± 1 Ma.

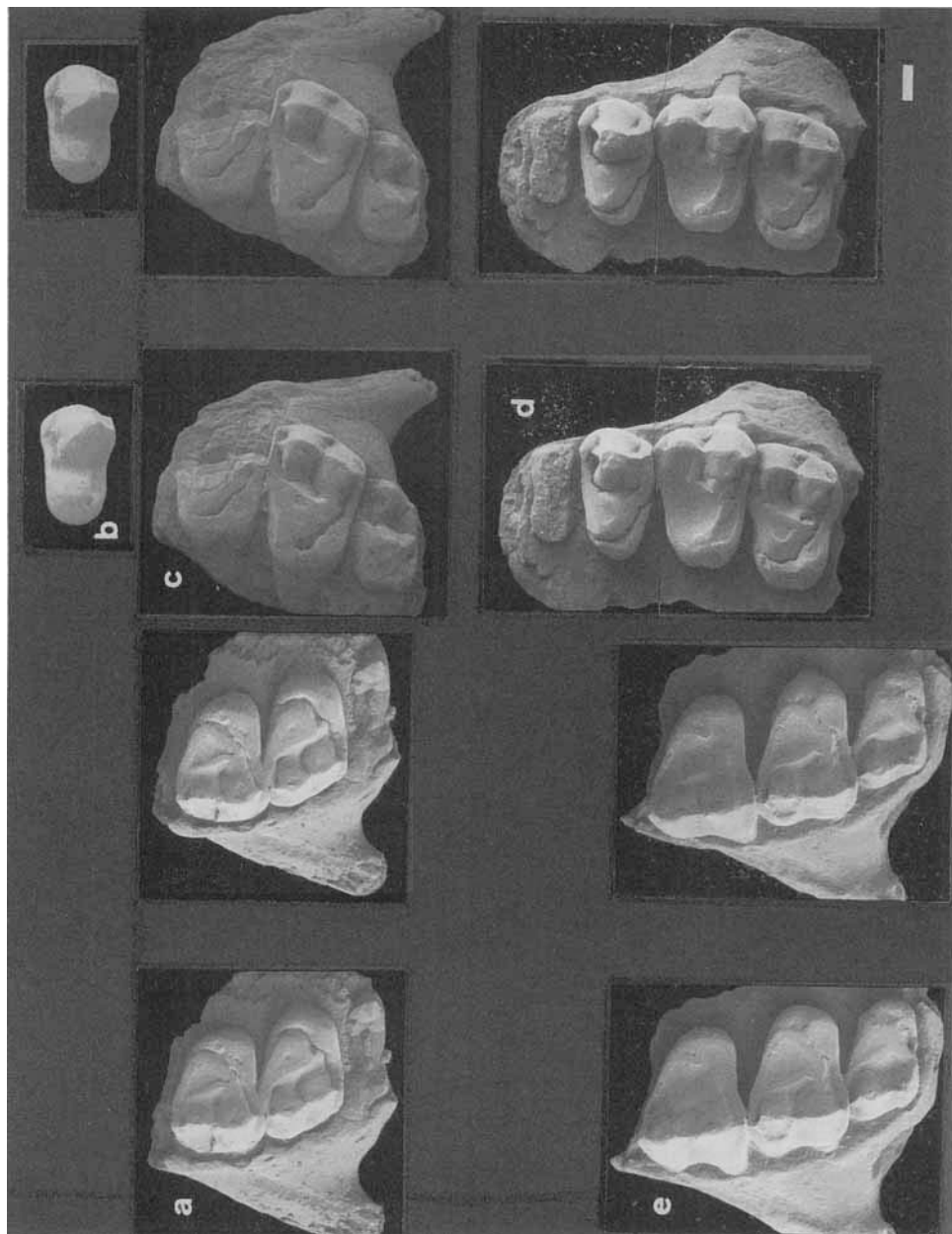


Fig. 3. Scanning electron micrographs of upper dentition of *Bransisella boliviana*. **a:** MNHN-Bol-V 3460, right $M^{1,2}$ and root for M^3 . **b:** MNHN-Bol-V 3466, left P^3 . **c:** MNHN-Bol-V 3467, left $M^{2,3}$ and lingual half of M^1 . **d:** Holotype, left P^4 – M^2 and roots for P^3 . **e:** UF27887, right M^{1-4} . Stereo pairs. Scale = 1 mm.

TABLE 1. Referred specimens and new materials

Referred specimens which have been discovered previously:		
Number	Description	Site
PU 21861 ^a	Left mandibular fragment with M ₂ and alveoli of P ₄ , M ₁ , and M ₃	Tapial Pampa
UF 27887 ^b	Right maxillary fragment with M ¹⁻³	Tapial Pampa
UF 27888	Right mandibular fragment with M ₂ and alveolus of M ₃	Tapial Pampa
UF 91399	Right mandibular fragment with M ₂ and erupting M ₃	Tapial Pampa
New material:		
Number	Description	Site
MNHN-Bol-V 3460 ^c	Right maxillary fragment with M ^{1,2} and root for M ³	Los Cactus
MNHN-Bol-V 3463	Left mandibular fragment with M ₁ and roots for P _{3,4}	Los Cactus
MNHN-Bol-V 3464	Right mandibular fragment with M ₂ and alveolus for M ₃	Los Cactus
MNHN-Bol-V 3465	Right P ₂ and mandible with M _{1,2} , unerupted P ₃ , and alveoli for dP ₂₋₄	Los Cactus
MNHN-Bol-V 3466	Left P ³ or ²	Campsite-Los Cactus
MNHN-Bol-V 3467	Left maxillary fragment with M ^{2,3} and lingual half of M ¹	Campsite-Los Cactus
MNHN-Bol-V 3468	Isolated left M ₁ and M ₂	Campsite
MNHN-Bol-V 3469	Right mandibular fragment with M _{1,2} and alveoli for dP _{2,3} and P ₄	Campsite
MNHN-Bol-V 3471	Right mandibular fragment with M _{1,2}	Opposite side of campsite river
MNHN-Bol-V 3473	Left mandibular fragment with roots of P ₃ -M ₁	Opposite side of campsite river

^a PU, Princeton University.^b UF, University of Florida.^c MNHN-Bol-V, Museo Nacional de Historia Natural, Bolivia; vertebrate collection.

Diagnosis

Dental formula: 2?1?3.3. The molar size is subequal to that of extant *Aotus* (see Figs. 6,7). The P^{3,4} bicuspid has a large paracone and a rather small protocone. The M^{1,2} has three main cusps (protocone, paracone, and metacone), which are massive and bulbous, being closely, not marginally, situated with respect to each other. There is a small but distinct hypocone present on the well developed distolingual cingulum, and no paracoenule. The metaconule is usually distinct on M¹, but it obscure on M². The M³ has a large protocone and paracone, much smaller metacone, and a distinct distolingual cingulum without hypocone. The P₂ unicuspid has a continuous basal lingual cingulum. Lower molars are rather high crowned. Like the upper molars, M_{1,2} has four main cusps (protoconid, metaconid, hypoconid, and entoconid), which are massive and bulbous, being closely, not marginally, situated with respect to each other, and no paraconid. A small hypoconulid is sometimes present on M₂. The talonid basin is very deep and narrow, and lower than the trigonid. On M_{1,2} the lingual half of the distal margin of the talonid slightly protrudes distally. M₃ is mesiodistally long, with the talonid tapering distally.

Description

P^{3,4} are bicuspid, with a large paracone and a lower protocone. A preprotocrista runs from the protocone to the parastyle. On P³ there is no distinct postprotocrista, while a distal cingulum runs around the protocone as far as its distolingual base (Fig. 3b). On P⁴, by contrast, the postprotocrista changes gradually to the distal cingulum, with a distinct distolingual cingulum (Fig. 3d). In occlusal view, P³ is pear shaped with the distal marginal line slightly concave, while P⁴ is almost oval. On P^{3,4} there are two buccal grooves mesial and distal to the paracone.

M^{1,2} have subequal-sized paracone and metacone, and a lower but moderately large protocone. These three cusps are bulbous and massive, and situated close to each other with a narrow, deep trigon basin. The distolingual cingulum is well developed with a small but distinct hypocone. The protocone and hypocone are completely separated by a deep sulcus, so there is no prehypocrista. M^{1,2} are narrower lingually than buccally, with a rather triangular profile in occlusal view. The protocone is more likely to be worn than the two other main cusps. Some specimens have a mesostyle on the styler area (M¹: 1/3; M²: 2/4). One M² specimen has a curious conule, just distal to the postproto-

crista (Fig. 3a). M^2 is slightly wider buccolingually than M^1 . The buccal marginal line of M^2 is more oblique than that of M^1 . On the styler shelf, there are two distinct buccal grooves, mesial to the paracone and distal to the metacone. There is no paraconule on $M^{1,2}$. On M^1 a small metaconule is observed in some specimens, while on M^2 there is no distinct metaconule. $M^{1,2}$ are three-rooted.

M^3 has a large paracone and protocone, and a much smaller or incipient metacone, with a distinct distolingual cingulum. There is no hypocone on the distolingual cingulum. M^3 is single- or incompletely double-rooted, although Wolff (1984) describes it as three-rooted. $M^1 < M^2 >> M^3$.

P_2 is unicuspid, with a high, conical protoconid and a complete basal lingual cingulum (Fig. 4b). The occlusal outline is rather oval with a long axis in the mesiobuccal-distolingual direction. The preprotocristid and protolophid form well-developed crests. All lower premolars are single-rooted.

The high-crowned lower molars, like the upper molars, have four bulbous, massive main cuspids, which are situated close to each other with narrow, deep trigonid and talonid basins (Figs. 4,5). The trigonid is slightly higher than the talonid. The lower molars have no paraconid. M_1 has no hypoconulid, while M_2 sometimes has a small hypoconulid. On M_3 , the talonid tapers distally but there is no distinct hypoconulid. On M_1 , the trigonid is slightly narrower than the talonid, while on M_2 they are subequally wide and the talonid is rather long mesiodistally. On all molars, the protolophid and cristid obliqua, both of which are rather low, run almost transversely and mesiodistally, respectively. On $M_{1,2}$, the lingual half of the distal margin protrudes slightly distally. The ectoflexid is quite deep, with a buccal conulid (M_1 : 2/2; M_2 : 3/7), while there is no distinct buccal cingulid. $M_{1,2}$ is double-rooted and M_3 is single-rooted. One M_2 specimen has a curious cuspid at the center of the talonid basin (Fig. 4d).

DISCUSSION

Variability of *Branisella* and validity of "*Szalatavus*"

Since the first specimen was discovered in the 1960s, all the fossil primates discovered

in the same locality, Tapial Pampa of the Salla-Luribay basin, have been referred to the same taxon, *Branisella boliviana* (Hoffstetter, 1969, 1974; Rosenberger, 1981; Wolff, 1984). Recently, however, several workers reviewed these primate materials and described some of them (UF27887, 27888, and 91399; Figs. 3a,4e, Table 2) as a new taxon, "*Szalatavus attricuspis*," based on the combination of the following characters: in "*Szalatavus*" $M^{1,2}$ is more triangular than in *Branisella* in occlusal view, with a relatively small hypocone on the less developed lingual cingulum, producing larger interproximal embrasures; the mandible is more gracile and shallower, and the muzzle is much longer (Rosenberger et al., 1991b).

These distinguishing features are based on only three specimens, one maxillary and two mandibular fragments, and seem far from providing a sufficient definition for an independent genus for the following reasons (see Table 3). First, the characteristics of the "*Szalatavus*" upper molar depend greatly on the development of a distolingual cingulum: a less developed distolingual cingulum would render the occlusal view rather triangular, producing larger interproximal embrasures, and it would influence the size of the hypocone. All these characteristics are not independent of each other, but are closely linked to one another. Moreover, for example, M^1 of the newly discovered specimen, MNHN-Bol-V 3460 (Fig. 3a), closely resembles that of "*Szalatavus*," while M^2 of the same specimen has a well developed distolingual cingulum and a moderate hypocone, being different from M^2 of "*Szalatavus*."

Next, the lower molars of "*Szalatavus*" cannot be differentiated from those of *Branisella* by crown morphology. The only feature that distinguishes "*Szalatavus*" lower dentition from that of *Branisella* is the mandible depth below M_2 . However, the individual variation in platyrrhine mandibles is very large, probably because of the irregular ventral marginal line. It is incautious to regard only one specimen, PU 21861, as being representative of the *Branisella* mandible.

To date, fossils of all the Salla primates have been discovered in a very small area, and in almost the same horizon, the *Branisella* zone of MacFadden (1990), suggesting that the animals lived synchronologically

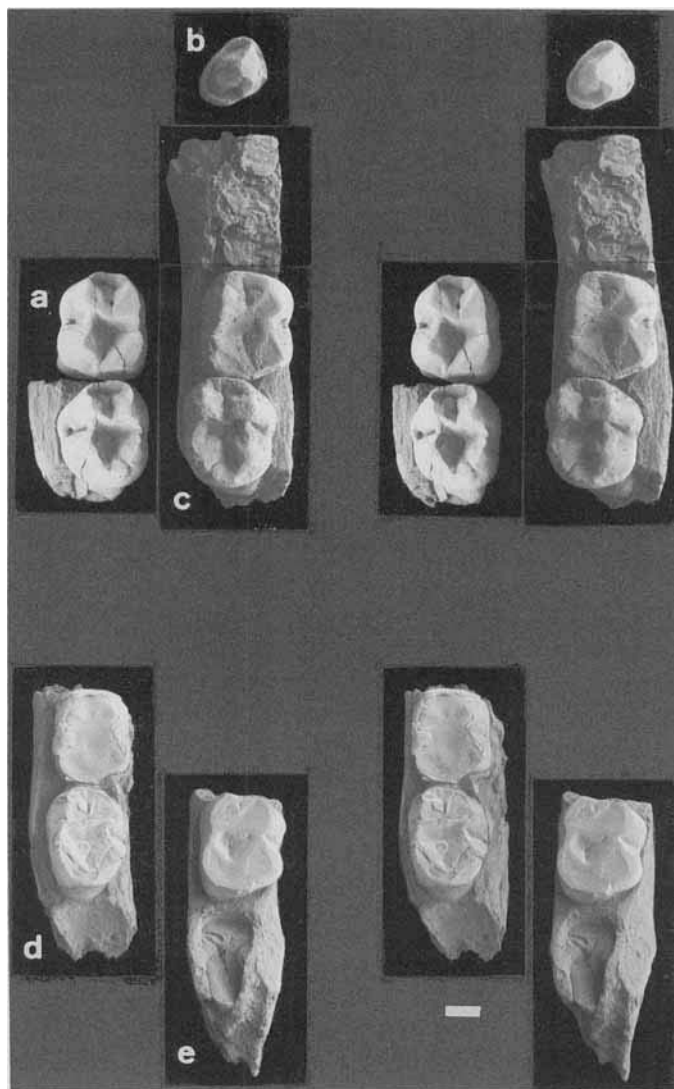


Fig. 4. Scanning electron micrographs of lower dentition of *Branisella boliviana*. **a:** MNHN-Bol-V 3468, left isolated M_1 and M_2 . **b:** MNHN-Bol-V 3465, right P_2 . **c:** MNHN-Bol-V 3465, right mandibular fragment with $M_{1,2}$, and alveoli for $dP_{3,4}(?)$. **d:** MNHN-Bol-V 3471, right mandibular fragment with $M_{1,2}$ (chemically damaged). **e:** UF27888, right mandibular fragment with M_2 and alveolus for M_3 . Stereo pairs. Scale = 1 mm.

and sympatrically in the late Oligocene. It would be unusual for two kinds of primate of the same size with similar dentition to live together sympatrically in a very small area.

In La Venta, Colombia, one of the most famous sites in South America that has yielded many primate fossils, many researchers have classified fragmentary materials into different taxa, and caused a taxonomical confusion. Takai (1994) dem-

onstrated that two same-sized fossil primates, *Neosaimiri* and "*Laventiana*," which were recovered from the same area, belonged to a single taxon, *Neosaimiri*, on the basis of more than 200 isolated teeth recovered from the same locality (Rosenberger et al., 1991a; Takai, 1994). Kay et al. (1987) also showed that the M^3 of *Stirtonia* has been wrongly identified as the upper molar of another taxon (Setoguchi, 1985). Moreover, a



Fig. 5. Scanning electron micrographs of lower dentition of *Branisella boliviana*. **a:** MNHN-Bol-V 3464, right mandibular fragment with M_2 and alveolus for M_3 . **b:** MNHN-Bol-V 3469, right mandible with $M_{1,2}$ and alveoli for $P_{3,4}$. **c:** MNHN-Bol-V 3463, left mandibular fragment with M_1 and roots of $P_{3,4}$. Stereo pairs. Scale = 1 mm.

recent dispute about the classification of two Miocene forms from La Venta, *Aotus din-densis* and *Mohanamico hershkovitzi*, suggests the difficulties encountered in identifying fossil taxa, even though rather complete mandibles have been preserved (Luchterhand et al., 1986; Setoguchi and Rosenberger, 1987; Kay, 1990; Rosenberger et al., 1990).

Paleontologists tend too easily to define a new taxon on the basis of a few fragmentary fossil specimens. Such classifications are not always incorrect and are sometimes adequate, but if there are no obvious morphological differences between two or more forms discovered in the same area and/or the same horizon, the forms should be treated as a single taxon. "*Szalatavus*" appears to be

TABLE 2. *Dental measurements of* *Branisella boliviana*

Upper Specimen	P ²		P ³		P ⁴		M ¹		M ²		M ³	
	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
MNHN 3460									2.64	3.97		
MNHN 3466			2.08	3.25					2.91	4.04	1.89	3.09
UF 27887							3.02	4.17	2.81	4.31	2.20	3.56
Holotype					2.13	3.66	2.98	3.91	2.75	3.96		
Lower Specimen	P ₂		P ₃		P ₄		M ₁		M ₂			
	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL		
								trd	tad		trd	tad
MNHN 3464										3.05	2.84	2.68
MNHN 3465	2.28	2.10					3.15	2.90	2.90	3.31	2.94	2.63
MNHN 3468							3.08	2.60	2.72	3.26	2.76	2.54
MNHN 3469										3.11	2.81	2.72
MNHN 3471							2.86			3.08		
PU 6510										3.03		2.39
UF 27888										2.99	2.70	2.61
UF 91399										2.94	2.59	2.38

MD, mesiodistal length (mm); BL, buccolingual width (mm); trd, trigonid width; tad, talonid width.

TABLE 3. *Distribution of characteristics of upper molars of* *Branisella*

		Holotype	UF 27887	MNHN-Bol-V 3460	MNHN-Bol-V 3466 & 3467
P ³	Lingual cingulum	—	—	—	B type
	Occlusal view	—	—	—	Pear like
	MD length (mm)	—	—	—	2.08
	BL width (mm)	—	—	—	3.25
P ⁴	Lingual cingulum	E type	—	—	—
	Occlusal view	Oval	—	—	—
	Buccal groove	Mesial & distal	—	—	—
	MD length (mm)	2.13	—	—	—
M ¹	BL width (mm)	3.66	—	—	—
	Occlusal view	Rectangular	Triangular	(Triangular?)	Rather triangular
	Lingual cingulum	(Not developed?)	Rather developed	Developed	Developed
	Hypocone	(Not developed)	(Not developed)	(Not developed)	Rather developed
	Metaconule	Incipient	Incipient?	Incipient	?
	Postprotoconule	Absent?	Absent	Incipient	Absent
	Buccal groove	Present	Shallow	Present?	?
	Mesostyle	Present	Absent	Absent?	Absent
M ²	MD length (mm)	2.98	3.02	2.84	—
	BL width (mm)	3.91	4.17	3.96	—
	Occlusal view	Rectangular	Rather triangular	Triangular	Rather triangular
	Lingual cingulum	Well developed	Not developed	Well developed	Well developed
	Hypocone	Small	Small	Moderate	Moderate
	Metaconule	Absent	Absent	Absent	Absent
	Postprotoconule	Present	Absent	Well developed	Absent
	Buccal groove	Present	Shallow	Present	Present
M ³	Mesostyle	Present	Absent	Absent	Present
	MD length (mm)	2.75	2.81	2.64	2.91
	BL width (mm)	3.96	4.31	3.97	4.04
	Occlusal view	—	Oval	—	Oval
	Distal cin.	—	Present	—	Present
	Hypocone	—	Absent	—	Incipient
	Main cusps	—	pr>pa>>me	—	pr>pa>>me
	Buccal groove	—	Mesial	—	Mesial
	MD length (mm)	—	2.2	—	1.89
	BL width (mm)	—	3.56	3.13	3.09

MD, mesiodistal; BL, buccolingual; pr, protocone; pa, paracone; me, metacone.

nothing more than a junior synonym of *Branisella*.

Reconstruction of the face of *Branisella*

Several workers considered *Branisella* a short-faced primate from the relatively small root of P² of the holotype (Hoffstetter, 1969, 1980; Szalay and Delson, 1979; Rosenberger, 1981; Fleagle, 1988; Conroy, 1990). However, newly recovered premolar specimens (MNHN-Bol-V 3466 and 3465, P³ and P₂, respectively; Figs. 3b, 4b) are not very small but are moderate in size, as compared with those of living medium-sized platyrrhines (Figs. 6a, 7a). The size of the anterior premolars does not support the reconstruction of an unusually short-faced primate for *Branisella* but suggests *Aotus*-like, slightly anteriorly reduced, dental proportions.

As Rosenberger (1981) proposed from the mandibular specimen of *Branisella* (PU 21861), the new mandibular specimen (MNHN-Bol-V 3469; Fig. 5b), which is the right half of a mandible, obviously shows evidence of symphyseal fusion: the anterior part of this mandible is quite robust and curves medially, demonstrating that this primate surely achieves the rank of a higher primate, as a platyrrhine. Moreover, the broken cross section of the mandibular symphysis reveals the presence of a horizontal shelf, a superior transverse torus. Among living and fossil platyrrhines, this feature is well developed in *Saimiri*, *Aotus*, *Callicebus*, and in most callitrichines, but it is not so apparent in *Cebus*, pitheciines, and atelines. This feature is not observed in extant *Alouatta* but is found in *Stirtonia*, a middle Miocene ancestor of *Alouatta* discovered in Colombia (Stirton, 1951). Fleagle and Kay (1987) reported this feature in early Oligocene parapithecids from the Fayum, Egypt, namely, *Apidium* and *Parapithecus*. Below the superior transverse torus, a small but distinct genioglossal pit is observed, which is also present in parapithecids and in *Stirtonia* (Stirton, 1951) but is not apparent in living *Alouatta*. Therefore, the superior transverse torus and the genioglossal pit represent the primitive state in platyrrhine phylogeny, confirming the primitive nature of *Branisella*.

The *Branisella* mandible is rather shallow

anteriorly, resembling that of *Aotus*. The mental foramen in *Branisella* is situated below P_{2,3} as it is in most living platyrrhines, while in *Saimiri* it is usually situated rather anteriorly, for example, below C–P₂.

A callitrichine-like P₂

The newly discovered P₂ specimen (MNHN-Bol-V 3465; Fig. 4b) has some interesting features which suggest its close affinity with callitrichines: *Branisella* P₂ is unicuspid with a large, conical protoconid, lingually surrounded by a complete basal cingulum. In occlusal view, it is rather oval, with the long axis in the mesiobuccal–distolingual direction. A blade-like protolophid descends distolingually from the apex of the protoconid, without connecting to the lingual cingulum. There is no sign of a metaconid at the end of the protolophid.

The combination of such characteristics is usually seen in extant *Callimico*, *Saguinus*, *Aotus*, and in a middle Miocene form from Colombia, *Aotus dindensis* (Setoguchi and Rosenberger, 1987). In other callitrichines, *Cebuella* and *Callithrix*, and in *Callicebus*, the lower premolars are much longer diagonally. In extant *Cebus*, *Saimiri*, two middle Miocene forms from Colombia, *Neosaimiri* and *Mohanamico* (Lufterhand et al., 1986; Kay, 1990; Rosenberger et al., 1990), and in an early Miocene form from Patagonia, *Soriacebus* (Fleagle et al., 1987), the lingual cingulum is only rudimentarily developed at the mesiolingual face, so the protolophid descends continuously to the basal lingual face. Another early Miocene form from Patagonia, *Carlocebus*, has a more developed cingulum than that of *Soriacebus*, but its occlusal profile is not oval but rather distorted with the preprotocristid protruding more anteriorly (Fleagle and Bown, 1983; Fleagle et al., 1987; Fleagle, 1990). In pitheciines, the lingual cingulum is also poorly developed at the mesiolingual face and the protolophid is very short, so P₂ is very narrow buccolingually. In atelines, the lingual cingulum is well developed with connecting with the protolophid, and the occlusal profile is rather roundish. The close similarity between P₂ of *Branisella* and those of *Callimico* and *Saguinus*, which are regarded as more primitive taxa among callitrichines, suggests that

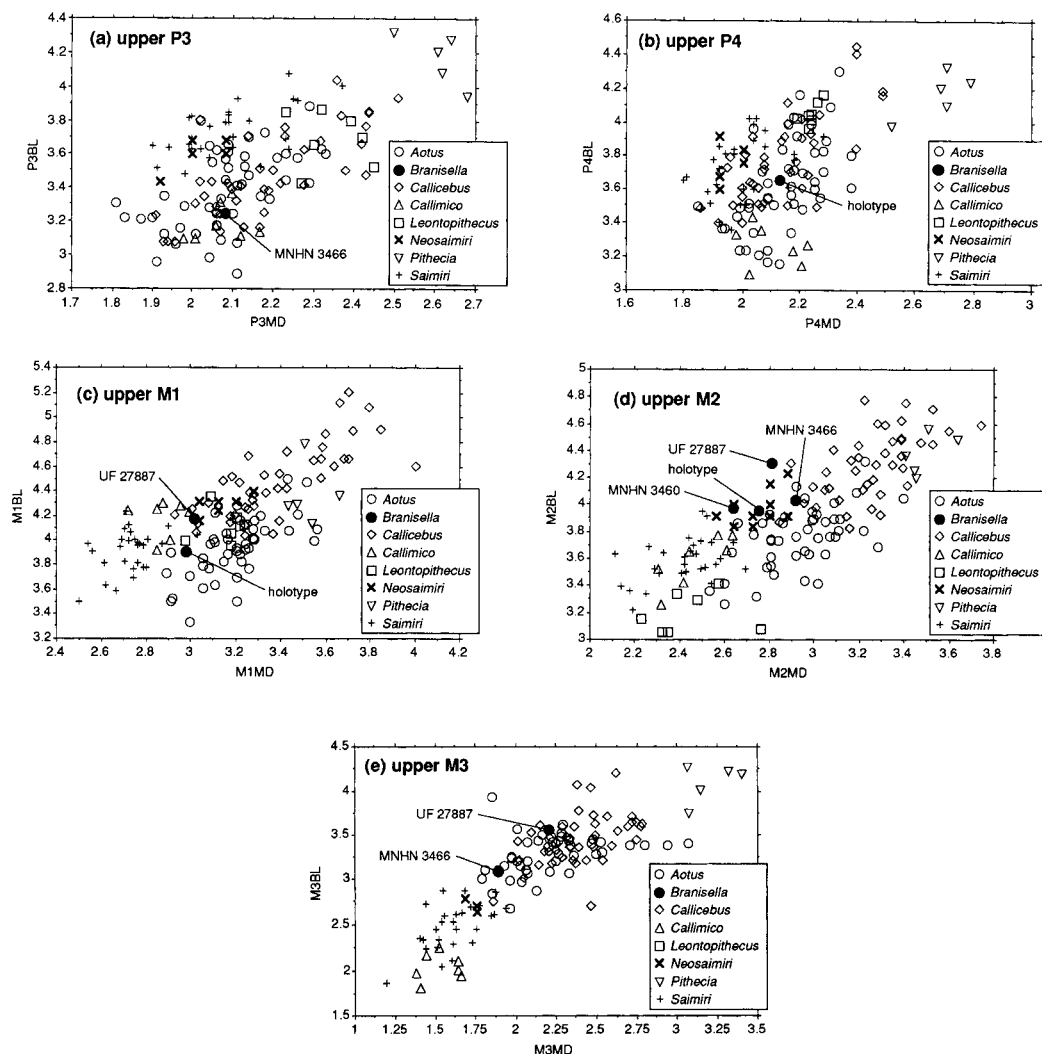


Fig. 6. Scatterplots of upper teeth of medium-sized platyrrhines. MD, mesiodistal length (mm). BL, buccolingual width (mm). a: P³. b: P⁴. c: M¹. d: M². e: M³.

Branisella shares derived P₂ characters with early callitrichines.

The cusp pattern of molars and curious conules

In the molars of *Branisella*, large, bulbous cusps are situated centrally, being very close to each other, so the trigon, trigonid, and talonid basins are quite small. In living platyrrhines, by contrast, the main cusps are situated more marginally. For example, in *Neosaimiri*, a middle Miocene form from Colombia, cusps of the lower molars are situ-

ated closer to each other than in its probable descendant, *Saimiri*, suggesting an evolutionary transformation whereby molar cusps have shifted marginally (Takai, 1994). Therefore, if the putative affinity between *Branisella* and callitrichines is real, the closely situated cusp pattern seen in *Branisella* molars should represent the primitive state of the platyrrhine dentition. The high molar crown and massive, bulbous cusps of *Branisella* can also be taken to represent the primitive state, suggesting an unspecialized omnivorous diet for primitive platyrrhines.

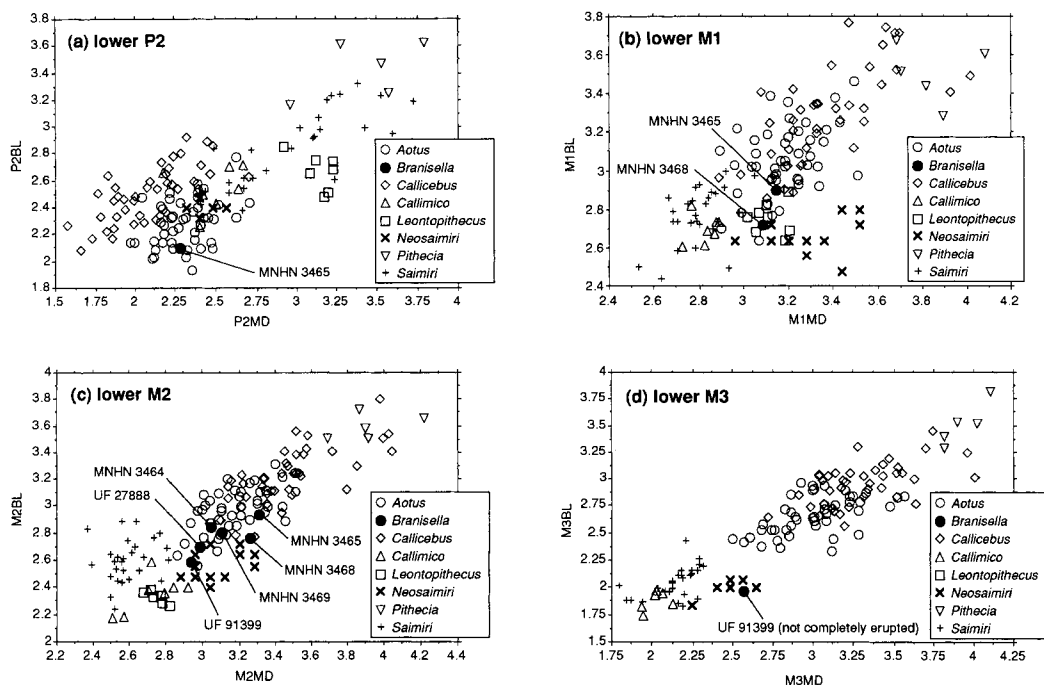


Fig. 7. Scatterplots of lower teeth of medium-sized platyrrhines. MD, mesiodistal length (mm). BL, buccolingual width (mm). **a:** P₂. **b:** M₁. **c:** M₂. **d:** M₃. The buccolingual width of M_{1,2} is not taken as the talonid but as the maximum.

One upper molar specimen (MNHN-Bol-V 3460; Fig. 3a) has a curious conule just distal to the postprotocrista. This accessory conule cannot be a metaconule for the following two reasons: first, it does not appear on but is squeezed out from the postprotocrista, forming a kind of protuberance; second, all M¹ specimens have an obvious metaconule on the postprotocrista. Such a curious, accessory conule is never seen in extant platyrrhines, but a similar structure was observed in one Miocene form from La Venta, Colombia (Meldrum, personal communication). Its phylogenetic significance is unknown to date. The development of a prehypocrista might be related to this conule, but the position of this conule seems a little buccal to the "normal" position of the prehypocrista.

One lower molar specimen (MNHN-Bol-V 3471; Fig. 4d) also has a strange conulid at the center of the talonid basin. Although this conulid is moderately worn, it seems to have no significant function in mastication. Herskovitz (1977) described this conulid as

a "plagioconulid," but did not mention which species have it. Among extant and extinct platyrrhines, such a conulid has never been observed. *Apidium*, an early Oligocene form from Fayum, Egypt, also has a curious cuspid, a "centroconid," on M_{1,2}, but this cuspid appears at the mesial end of the cristid obliqua, so there is no homologous relationship between the "plagioconulid" and the "centroconid" (Fleagle and Kay, 1987).

Structure and evolution of upper premolars

One of the most interesting features of *Branisella* is the upper premolar structure: the relationship between the lingual cingulum and hypocone. A newly discovered P³ (MNHN-Bol-V 3466, Fig. 3b) has neither a lingual cingulum nor a hypocone, as is often the case in small platyrrhines. By contrast, P⁴ of the holotype has an obvious distolingual cingulum without a hypocone, being separated from the postprotocrista-distocrista by a deep sulcus, which is never seen in plat-

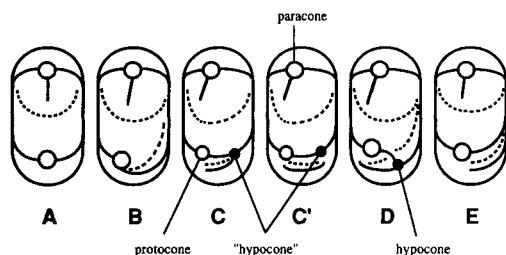


Fig. 8. Diagram of upper premolar structure, classifying the relationship between the lingual cingulum and hypocone into the following five patterns: **A**, neither a lingual cingulum nor a hypocone is present; **B**, neither a lingual cingulum nor a hypocone is present, and the distocrista runs around the protocone lingually; **C**, the lingual cingulum is present, joining the postprotocrista at the "hypocone" position or remaining at the lingual base (**C'**); **D**, the hypocone is present, often connecting with the protocone through the prehypocrista; and **E**, the distolingual cingulum is present, not connecting with the postprotocrista, and there is no hypocone. Occlusal view of upper left premolars: anterior is to the left, and lateral is at the top.

rrhines. In several platyrrhines, of course, the upper premolar often has a lingual cingulum, distally joining the postprotocrista or remaining as a small cingulum at the lingual face of the protocone. The basic structure of the lingual cingulum of the *Branisella* P^4 seems completely different from those of living platyrrhines.

Among living and fossil platyrrhines, there are several patterns of the lingual cingulum and hypocone on upper premolars. Here, we classify the upper premolar structures of platyrrhines into five types (Fig. 8): **A**: Neither a lingual cingulum nor a hypocone is present. This pattern is usually seen in most platyrrhine premolars. In this type the protocone is usually vestigial (e.g., P^2 of most platyrrhines and $P^{3,4}$ of *Cebus*). **B**: Neither a lingual cingulum nor a hypocone is present; the distocrista runs around the protocone lingually (e.g., $P^{3,4}$ of callitrichines, and P_4 of *Aotus*, *Alouatta*, and *Ateles*). **C**: The lingual cingulum is present, joining the postprotocrista at the "hypocone" position or remaining at the lingual base (e.g., $P^{3,4}$ of *Saimiri*, *Callicebus*, *Saguinus*, *Leontopithecus*, *Callimico*, and *Cebupithecia*, a middle Miocene form from La Venta, Colombia). **D**: The hypocone is present, often connecting with the protocone through the prehypocrista.

crista (e.g., $P^{3,4}$ of *Neosaimiri*, a middle Miocene form from La Venta, Colombia). **E**: The distolingual cingulum is present, not connecting with the postprotocrista, and there is no hypocone (e.g., P^4 of *Branisella*).

From the evidence of a tiny P^2 alveolus in the holotype of *Branisella*, Rosenberger (1979, pp. 165–166) describes the morphotype of platyrrhine upper premolars as follows: "... a small, unicuspid P^2 , having some lingual cingulum development may be the primitive state of platyrrhines and ceboids." However, judging from the size of P_2 and the well developed protocone of P^3 , the *Branisella* P^2 should be moderate sized and bicuspid. In other words, there is no adequate reason to presume that the morphotype of platyrrhine upper premolars is small and unicuspid with some lingual cingulum. However, we must ask what the structural difference between *Branisella* P^3 and P^4 means. Before discussing this question, we must examine homologies with the "hypocone" of the C type.

It has not yet been determined whether the "hypocone" of the C type is homologous to the hypocone of the D type. The latter hypocone is obviously derived from the lingual cingulum, as indicated by the traditional definition of a true hypocone, while the former "hypocone" seems to be derived from the postprotocrista, which is traditionally treated as a pseudohypocone.

Among living platyrrhines, *Callicebus* sometimes has an intermediate state between C and D types, suggesting a transformational series between these two types. Takai (1994) supports an evolutionary relationship between *Neosaimiri* (D type) and *Saimiri* (C type) and an evolutionary transformation from the D type to the C type: that is, the hypocone and prehypocrista of the D type have shifted buccally to form the postprotocrista of the C type, producing a lingual cingulum. In this transformation scenario ($B \rightarrow D \rightarrow C$), the D-type hypocone is derived from the distocrista of the B type, and the C-type lingual cingulum is originally derived from the mesiolingual part of the B-type distocrista. This hypothesis, of course, is based on an assumption of homologies with the "hypocone" of the C type.

There is another possibility: that is, the D

type has no relationship to other types and the E type has produced the C type, implying that the "hypocone" of the C type is not a true hypocone. This hypothesis requires a very daring assumption: that is, the "hypocone" of the premolars in most living platyrrhines should be a pseudohypocone, if we admit a true hypocone of the D type. However, the presence of an intermediate form in upper premolars of *Callicebus* does not support this scenario.

Supposing that we admit the evolutionary transformation as being of the B→D→C type, there remains another serious question: what is the E type of *Branisella*? Did the E type produce the B type? If the E type produced B and subsequent D and C types, the lingual cingulum must have disappeared during the step from E to B and occurred again in D and C types. This scenario is not parsimonious. Therefore, it is reasonable to regard P⁴ of the holotype of *Branisella* as an individual variation, and to assume that the newly discovered P³ is closer to the morphotype of platyrrhine upper premolars.

With respect to the upper premolar pattern, living platyrrhines are classified into two groups. The first group has neither a lingual cingulum nor hypocone. It includes pitheciines, atelines (including *Alouatta*) (A, B types), and *Cebus* (A type). The second group has a lingual cingulum with a "hypocone" often on P³ or P⁴, for instance, in *Saguinus*, *Callimico*, *Leontopithecus*, *Callicebus*, *Saimiri*, and *Aotus* (C type). This dichotomous classification is not rigid but is suggestive of the evolutionary tendency in each group. The *Branisella* P³ (a variation of the B type) does not show transformational signs of the C type, as already mentioned above; its large protocone suggests a close resemblance to rather primitive callitrichines, such as *Callimico* and *Saguinus*.

Phyletic position of *Branisella* in platyrrhine phylogeny

Since the first specimen was discovered at Salla in the 1960s, many researchers have pointed out a close resemblance between the upper molars of *Branisella* and those of the living squirrel monkey, *Saimiri*, implying a *Saimiri*-like ancestral platyrrhine molar morphotype (Rosenberger, 1979; Gingerich, 1980; Orlosky, 1980; Fleagle, 1988; Conroy,

1990). As already mentioned, however, the crown morphology of other teeth in *Branisella* does not support this view. For example, the upper and lower premolars of *Branisella* are obviously similar to those of primitive callitrichines, such as *Callimico* or *Saguinus*, rather than to those of *Saimiri*. In addition, the high-crowned lower molars with centrally situated cuspids of *Branisella* no more resemble those of *Saimiri* than they do those of any living platyrrhines. The morphological discrepancy between "*Saimiri*-like" upper molars and non-*Saimiri*-like other teeth seen in *Branisella* necessitates reexamination of the interpretation of *Branisella*'s upper molars.

Recently, Rosenberger and coworkers (Rosenberger et al., 1990, 1991b) have discussed the validity of the supposed morphological resemblance between upper molars of *Branisella* and *Saimiri*. According to them, in *Saimiri* the hypocone and lingual region of the upper molars are secondarily enlarged, and what remains primitive about the morphology is the low position of the cusp relative to the trigon. In *Branisella*, on the other hand, the hypocone is much smaller and low, which is the morphotypic pattern in platyrrhine phylogeny. Their conclusion is correct insofar as the morphological resemblance between *Saimiri* and *Branisella* is superficial. As they insist, the most essential morphological difference between them is not the size of the hypocone but the development of the lingual region, that is, the lingual cingulum and talon area. In *Saimiri*, the upper molars have a relatively small hypocone and a well developed talon area, in contrast to the poorly developed talon area of *Branisella*. However, their conclusion about the character polarity is problematic. They suggest that the small hypocone and talon area of *Branisella* reflects a primitive state of platyrrhine phylogeny and that the lingual region of *Saimiri* has secondarily enlarged, on the basis of the hypothesis that a small to moderate, low hypocone is the morphotypic pattern (Rosenberger et al., 1990, 1991b). The most problematic issue in their entire discussion is this premise.

Branisella is, at present, the oldest recorded fossil platyrrhine, and thus the upper molar of *Branisella* has been regarded as the primitive state in platyrrhine phylogeny.

However, several outgroup taxa, such as parapithecids, early Oligocene forms from the Fayum, and *Dolichocebus* and *Carlocebus*, two early Miocene forms from Patagonia, obviously have a well developed talon area and a relatively large hypocone, suggesting that primitive platyrrhine upper molars have a large talon area with a moderate to large hypocone.

The estimated morphological transformation in the *Neosaimiri*–*Saimiri* lineage also supports this conclusion. According to Takai (1994), *Neosaimiri*, a probable middle Miocene ancestral taxon for extant *Saimiri*, has relatively rectangular upper molars ($M^{1,2}$) with a larger talon area and hypocone, while *Saimiri* $M^{1,2}$ are reduced in size and the main cusps have shifted marginally. So, if the phylogenetic relationship between *Neosaimiri* and *Saimiri* is real, a well developed talon area represents the primitive state in this lineage.

Thus, both out-group comparison and fossil evidence support the hypothesis that an upper molar with a large talon area and a moderate to large hypocone is the ancestral platyrrhine molar morphotype. Upper molars of *Branisella* do not exhibit this ancestral pattern but have a reduced, not undeveloped, talon area and hypocone, so they can be regarded as more developed, more callitrichine like, than the hypothetical ancestor. The geologic age of *Branisella* is late Oligocene or earliest Miocene, which is not very much older than those of some Patagonian forms. In addition, the oldest form does not always reveal the most primitive state. Rosenberger (1979) concluded that a small to moderate hypocone is ancestral in platyrrhine phylogeny on the basis of neontological studies, and other workers accepted his conclusion without major criticisms (Ford, 1986; Kay, 1980). However, discussions of the morphotype of platyrrhine upper molars are still incomplete.

The present new materials suggest a different interpretation; in the evolution of the callitrichine clade, a primitively *Branisella*-like upper molar reduced its lingual cingulum and hypocone as a first step. Next, the third molars were reduced, and finally each cusp was reduced and shifted marginally. The phyletic position of *Branisella* in platyrrhine phylogeny is an ancestral group that

produced ancestral, primitive callitrichines, that is, the common ancestor for *Callimico* and other callitrichines. The common ancestor for all platyrrhines, preserving a large talon area and hypocone, should be discovered someday in early or middle Oligocene sediments, or in earlier deposits, in South America.

Today, the phylogenetic relationships among extant platyrrhines are still obscure although many morphologists are advocating their own phylogenetic hypotheses. Most of them admit three main groups in extant platyrrhines, callitrichines, pitheciines, and atelines, but they do not agree on the relationships among these three groups and the phyletic positions of four other genera, *Saimiri*, *Cebus*, *Aotus*, and *Callicebus* (Ford, 1986; Kay, 1990; Rosenberger 1981, 1984). None of them have included *Branisella* on their phylogenetic trees, so their views of the phyletic position of *Branisella* are unknown. However, they all regard *Branisella* as a rather primitive taxa in platyrrhine phylogeny, and many of them have traditionally regarded the upper molars of *Saimiri* as the most primitive among those of living platyrrhines. However, such a traditional, general view is not supported by several workers.

Recent molecular biological studies also suggest another phylogenetic tree, with trichotomous branching of *Saimiri*, *Cebus*, and *Aotus* (Schneider et al., 1993). The hypothetical *Branisella*–*Saimiri* lineage as the ancestral platyrrhine morphotype is no longer sufficiently well supported. As newcomers from Africa (?), platyrrhines radiated adaptively into Neotropical forests during the early to middle Oligocene and probably produced many ancestral taxa explosively. The branching speed of each group must have been so rapid that the branching order is unclear. The phyletic position of *Branisella* is not at the root of the platyrrhine phylogenetic tree but at the base of the callitrichine clade.

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